MONOMORIUM MINIMUM SPECIES GROUP: GYNE NUMBER AND LONGEVITY (HYMENOPTERA: FORMICIDAE)[1]

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ABSTRACT: Gyne number is reported for 13 species of the *Monomorium minimum* species group; life span, and worker mortality rates are presented for 5 species: *Monomorium cyaneum*, *M. emarginatum*, *M. minimum*, *M. trageri*, and *M. viride*. Most species appear able to establish colonies haplometrotically; most exhibit presumed secondary polygyny. Average gyne lifespans (under laboratory conditions) ranged from 1.08 years (*M. minimum*) to 7.54 years (*M. emarginatum*). Worker longevity for *M. cyaneum* ranged up to 1.4 years.

The ant genus *Monomorium* is represented by over 350 species (Bolton, 1995). There is no information concerning basic biology (such as number of gynes per colony and life span of gynes and workers) of most species. Keller (1998) conducted an extensive literature review and incorporated unpublished information regarding ant gyne life spans and related factors. Of the 53 ant species he discussed, only one species (*Monomorium pharaonis* (Linnaeus)) was included (Peacock and Baxter, 1950; Peacock et al., 1955). Keller's work expanded on the known life spans of 31 ant species' provided by Hölldobler and Wilson (1990: 169). Bolton (1995) listed over 9,500 species of ants.

The purpose of Keller's research was, "to test evolutionary theories on aging by investigating whether the evolution of eusociality had been paralleled by an increase in queen life span..." This is the expected pattern if life span is influenced by extrinsic mortality factors (Keller, 1998: 236). A side result was the confirmation of the paucity of knowledge of this aspect of basic ant biology. Comparative theories are difficult to evaluate when there are limited observations within a large and diverse group.

This publication provides longevity data for *Monomorium cyaneum* Wheeler, *M. emarginatum* DuBois, *M. minimum* (Buckley), *M. trageri* DuBois, and *M. viride* Brown. These are the first recorded observations for multiple members of the *minimum* species group (DuBois, 1986) for colonies kept under similar laboratory conditions. Although colonies were collected at different times, all were subjected to a similar regimen in the laboratory.

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Information concerning the number of queens per colony is included for members of the *Monomorium minimum* species group. This information is based principally from information gleaned during my revision (DuBois, 1986) and from subsequent field collections. Although isolated studies have reported gyne counts for a few species, this is the first time all species (within this group) have been included and compared.

METHODS AND MATERIALS

Longevity Study — Colonies of each species were collected and transported to the laboratory for study. Locality data for each colony is presented in Appendix A. Each colony was isolated in Fluon® coated chambers and provided suitable habitat (water filled test tubes wrapped with red cellophane as described in DuBois and DuBois, 1994). Ants were fed a combination of artificial ant diet (Hölldobler and Wilson, 1990: 632), a 50:50 mixture of honey and water, and chopped insects (typically grasshoppers, cockroaches, and Lepidoptera larvae). Observations were made weekly. Any dead individuals were removed and enumerated. Each species was identified by examination of both gyne and worker corpses. Identifications were made using DuBois (1986) and comparison with previously identified specimens. Voucher specimens were retained in the author's personal collection. Regression analyses were conducted for each colony to identify mortality rates in the laboratory. Colonies were maintained until all individuals had died. The final dates were recorded and life spans were calculated from the initial date of colony collection. In some cases, workers lived significantly beyond the death of the gyne. In these instances, an attempt was made to determine worker life span.

Gynes per Colony Study — Records were extracted from the author's personal collection of *Monomorium* coupled with notes made while examining museum collections during revision of this group. Only those collections that contained dealate gynes were counted. As with all collections, the observed number of gynes is presumed to represent the minimum found in each colony; others may have escaped detection. No effort was made to determine whether all gynes were fully fertile and inseminated. The issue of functional polygyny remains open for these species.

Literature records were examined to determine additional information regarding the number of gynes per colony (for example, Bhatkar, 1992). The data presented by Peacock and Baxter (1950) was subjected to the same statistical analyses.

RESULTS

Number of Gynes per Colony (Tables 1 and 2).

Longevity Study — For each species examined, the number of gynes per observed colony was noted. The total number of corpses removed confirmed this count. Statistics (average, standard deviation, and standard error of the mean) were calculated to provide the basis for comparisons. The number of colonies observed (n) is listed after the name of each species.

Table 1. Gynes per colony observed.

Species	Average	Min – Max	Standard Deviation	Standard Error
M. cyaneum (n =15)	3.93	1 – 15	4.008	1.0349
M. emarginatum (n = 1)	4	N/A	N/A	N/A
M. minimum (n = 5)	1	1	0.000	0.000
M. trageri (n = 4)	7	3 – 15	5.477	2.7386
M. viride (n = 12)	1.75	1 – 4	1.055	0.3046

Field Collections and literature records — Each species is listed with the number of gynes per collected colony. Collections containing only workers or reproductives were eliminated. Statistics (average, standard deviation, and standard error of the mean) were calculated. The number of colonies observed (n) is listed. Peacock and Baxter's (1950) data for *Monomorium pharaonis* is presented at the bottom of this table. Only the original data representing field collections (for baited and trapped colonies with dealate gynes) was used to calculate these statistics.

Table 2. Gynes per field collection.

Species	Average	Min – Max	Standard Deviation	Standard Error
M. compressum (n = 2)	2.5	2 – 3	0.707	0.5000
M. cyaneum (n = 26)	2.8	1 – 12	3.020	0.5923
M. ebeninum (n = 13)	3.3	1 – 10	2.983	0.8273
M. emarginatum (n = 4)	4.3	1 – 11	4.717	2.3585
M. ergatogyna (n = 24)	4.9	1 – 20	5.445	1.1114
M. marjorae (n = 1)	1.0	N/A	N/A	N/A
M. inquilinum (n = 1)	1.0	N/A	N/A	N/A
M. minimum (n = 65)	2.4	1 – 23	3.432	0.4257
M. pergandei (n = 1)	7.0	N/A	N/A	N/A
M. talbotae (n = 1)	8.0	N/A	N/A	N/A
M. trageri (n = 3)	4.0	1 – 10	5.196	3.0000
M. viride (n = 17)	6.5	1 – 64	15.038	3.6472
M. wheelerorum (n = 12)	1.0	1 – 1	0.000	0.0000
M. pharaonis (n = 10)	26.8	2 – 110	37.416	11.8320

Observed Workers Produced (per Colony) and Mortality (Tables 3 & 4).

Dead workers were removed weekly from each colony and enumerated. Since some workers were undoubtedly eaten before they could be removed, these calculations represent the lower boundary of total workers. Colony count (n) is provided in Table 1. Dead workers provide an indication of the reproductive capacity of each colony over the life of the colony (Table 3). This data also provides an indication of worker mortality under controlled laboratory conditions (fairly constant climate, consistent food supply and lack of predators) (Table 4).

Table 3. Workers produced per colony.

Species	Average	Min – Max	Standard Deviation	Standard Error
M. cyaneum	655.40	20 – 1323	388.724	100.3681
M. emarginatum	1658.00	N/A	N/A	N/A
M. minimum	329.80	101 – 773	264.321	118.2080
M. trageri	845.25	389 – 1560	502.345	251.1724
M. viride	785.17	87 – 2250	605.040	174.6601

Table 4. Weekly worker mortality.

Species	Number of weeks observed	Average	Standard Deviation	Standard Error
M. cyaneum	775	13.0	8.547	2.207
M. emarginatum	76	21.8	0.000	0.000
M. minimum	160	10.8	6.936	3.102
M. trageri	267	12.7	7.249	3.625
M. viride	552	18.5	12.416	3.584

Observed Adult Gyne Life Span (days) (Table 5).

Observed life span was calculated from the date of colony collection until the date of observed death of the last gyne for each colony. Since workers are unable to reproduce, colonies were doomed from the point of the last gyne's death. This calculation is presented as it represents a boundary with respect to the longevity of each colony. Individual gyne life spans were also recorded, but are not presented herein (details can be obtained by contacting the author directly). Since colonies were well established prior to collection, the actual life span of the colony may have been one or two years beyond what was observed in the laboratory.

Table 5. Observed adult gyne life span (days).

Species	Average	Min – Max	Standard Deviation	Standard Error
M. cyaneum	632	207 – 927	203.956	58.8769
M. emarginatum	2755	N/A	N/A	N/A
M. minimum	395	294 – 778	214.390	95.8783
M. trageri	546	403 – 674	111.101	55.5503
M. viride	451	118 – 713	198.671	57.3512

Observed Adult Worker Life Span (days) (Table 6).

Worker life span was calculated from the date the last gyne perished until the last worker perished. This represents an absolute minimum life span and assumes the worker eclosed on the day the last gyne perished. Calculations were only made on colonies where workers outlived gynes.

Table 6. Observed adult worker life span (days).

Species	Average	Range	Standard Deviation	Standard Error
M. cyaneum (n=7)	239	14 – 516	196.224	74.1658
M. minimum (n=1)	14	N/A	N/A	N/A
M. trageri (n=1)	182	N/A	N/A	N/A
M. viride (n=6)	54	14 – 83	24.850	10.1448

DISCUSSION

Gynes per colony — Bhatkar (1992) reported 2 – 38 physogastric gynes per colony of *M. minimum* in Texas and Louisiana. Voucher specimens could not be located to confirm this identification. Most colonies were presumed to have a single foundress with secondary adoption of additional gynes. Gregg (1944) reported 12 – 14 gynes per colony of *M. minimum* in the Chicago region. Dennis (1938) reported 12 – 15 gynes per colony for the same species in Tennessee. Gregg (1945) reported 64 gynes in a colony of *M. viride* in Florida and a single gyne in a colony of *M. cyaneum* in Arizona. Brown (1943) reported 1 – 5 gynes per colony of *M. viride* in New Jersey.

Although the sample sizes are different, the following comparison is attempted for those species within the *minimum* group. Fundamental assumptions are made about the distributions of gynes: they are normally distributed and that the observed mean and standard deviation are reasonably close to the population mean (μ) and standard deviation (σ). This would imply that 99.7% of all observations would fall within 3 standard deviations of the mean and 95.4% of all observations would fall within 2 standard deviations of the mean. The following formula was applied to determine raw scores for each species observed for corresponding z scores of 3 and 2 (resulting in Table 7):

$$x = z\sigma + \mu$$

Where: x = raw score, z = z score, σ = population standard deviation, and μ = population mean.

Table 7. Raw scores for gynes per colony.

Species	Raw Score (z = 2)	Raw Score (z = 3)
M. compressum (n = 2)	3.91	4.62
M. cyaneum (n = 26)	10.30	13.72
M. ebeninum (n = 13)	9.27	12.26
M. emarginatum (n = 4)	12.37	16.46
M. ergatogyna (n = 24)	15.81	21.25
M. marjorae (n = 1)	N/A	N/A
M. inquilinum (n = 1)	N/A	N/A
M. minimum (n = 65)	8.98	12.31
M. pergandei (n = 1)	N/A	N/A
M. talbotae (n = 1)	N/A	N/A
M. trageri (n = 3)	16.02	21.18
M. viride (n = 17)	27.78	39.41
M. wheelerorum (n = 12)	1.00	1.00
M. pharaonis (N = 10)	101.63	139.05

For each species listed in these tables, the raw scores would indicate the maximum number of gynes expected within 2 or 3 standard deviations. This would indicate a larger amount of polygyny in some species than others (particularly *M. pharaonis*).

Workers produced per colony — Several authors have commented on the large colony size for many of the *minimum* species group species. However, there do not appear to have been any investigations into worker mortality or numbers of workers produced for the five species (*M. cyaneum*, *M. emarginatum*, *M. minimum*, *M. trageri*, and *M. viride*) discussed herein. With relatively low worker mortality for all species observed (11 – 22 workers per colony per week) and individual queen's ability to produce large numbers of workers within a relatively short time span, it is not surprising that some colonies can become quite large.

Longevity — Previously reported observations indicated life spans for *M. minimum* (gynes lived approximately 1 year, workers lived approximately 4 months; DuBois, 1986: 81), for *M. ergatogyna* (gynes lived approximately 2 years, workers lived 4 – 8 months; DuBois, 1986: 91), and for *M. pharaonis* (gynes lived 39 weeks, workers lived 9 – 10 weeks, and males lived 3 – 8 weeks; Peacock and Baxter, 1950). Worker longevity observed here is similar to previously published observations. Most workers appear to live approximately 6 months. One notable exception is the extended life for *M. cyaneum* (1.4 years). Since workers from 4 colonies lived for nearly one year or longer, it would appear that this species has a significantly greater life span than other species examined to date. All *minimum* group species exhibit significantly longer life spans than that observed for the tropical tramp species *M. pharaonis*.

What was surprising were the long life spans of some of the observed queens (for example, *M. emarginatum* gynes with a life span exceeding 7 years). If one assumes the majority of colonies collected had persisted in the field for at least one year before collection (to allow them to grow to a size where they were noticed), the life span for most observed species is double what has been previously reported. Most gynes lived between one and 1.7 years in the lab, for a presumed total life of 2 to 2.7 years. Only *M. ergatogyna* had a previously reported life span of this length. Future research should concentrate upon additional tropical and subtropical species of *Monomorium* to ascertain whether *M. pharaonis* is unique with its short life span. Curiously, I could find no published life span information on *M. floricola*, a species that exhibits similar opportunistic nesting behaviors as *M. pharaonis*.

Overall comments — With the inclusion of the tropical tramp species, *Monomorium pharaonis* (previously studied), we now have longevity data for 1.7% of all described *Monomorium* species. Based on Keller's (1998) review of literature and non-published observations for other ant species, the sum of our knowledge of ant longevity now represents 0.61% of all known ant species. How long ants (gynes, workers, or males) live remains an area needing significant additional study. Comparative research such as that discussed by Keller (1998) may open more interesting lines of investigation once we have a clearer understanding of the entire range of variation with respect to how long ants live. This paper is intended to encourage others to continue documenting fundamental aspects of the biology of ants. Much work remains.

Appendix A

Locality information is provided for all colonies observed during this study. Locality information for additional field collections of *Monomorium minimum* and other species used to determine gyne numbers per colony is not presented below (to conserve space), but is available by contacting the author.

Monomorium cyaneum

Arizona: Pima Co., Santa Catalina Mountains, Loma Linda Picnic Area 7700', T11S R16E Sec 31, July 31, 1991, M. B. DuBois (MBD), J.R.DuBois (JRD), B.R.DuBois (BRD) Colonies: 1700 G, 1700 J, 1700 O, 1700 Q, and 1700 T.

Arizona: Pima Co., Santa Catalina Mountains, Inspiration Point 7700', T11S R16E Sec 31, August 6, 1991, MBD, JRD, BRD Colonies: 1704 A, 1704 D, 1704 E, 1704 F, 1704 H, 1704 J, 1704 L, 1704 M, 1704 N, and 1704 O.

Monomorium emarginatum

New York: Suffolk Co., Long Island (nest in sandy soil), May 17, 1987, Stefan Cover.

Monomorium minimum

Illinois: McLean Co., Funk's Grove, 600', T22N R01E Sec 19, May 23, 1992, MBD, J.D. Pratt.

Illinois: Mason Co., Revis Prairie, Easton 5.5 mi S, 0.25 mi W, T20N R07W Sec 26, August 30, 1992, MBD, F. Catchpole.

Illinois: Peoria Co., Jubilee College St. Park, Turkey Hollow 600', T10N R06E Sec 26, April 24, 1993, MBD Colonies: 1737 AA, 1737 AD, and 1737 AF.

Monomorium trageri

Florida: Alachua Co., 3.5 mi NE Gainesville, December 3, 1991, L. R. Davis, Jr. (LRD).

Florida: Clay Co., 1.3 mi S of Duval Co. line along Rte. 301, under bark of pine, May 17, 1992, LRD.

Florida: Columbia Co., Ichetucknee Springs St. Park, April 18, 1992, LRD.

Florida: Union Co., Worthington Springs, Santa Fe River, December 13, 1991, LRD.

Monomorium viride

Florida: Baker Co., Route 250, Vic. East Tower, Osceola Nat'l Forest, March 1, 1992, LRD Colonies: 1, 2.

Florida: Baker Co., Route 250 A, 0.25 mi N Route 90, Osceola Nat'l. Forest, March 1, 1992, LRD Colonies: 3, 4.

Florida: Baker Co., 1.3 mi W Duval Co., line along Route 90, May 17, 1992, LRD Colonies: 5, 6.

Florida: Union Co., Dukes, Along Route 18 A, 1.7 mi E Route 121, February 22, 1992, LRD.

Florida: Walton Co., Portland 1.1 mi NW, March 19, 1993, MBD, LRD, M. A. Deyrup (MAD) Colonies: 1732 C, 1732 D, and 1732 E.
Florida: Walton Co., Eglin Air Force Base, Freeport 4.5 mi NW, March 21, 1993, MBD, LRD, MAD Colonies: 1736 H and 1736 I.

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